Arenopsaltria nubivena
(Cicadidae: Cicadinae: Cryptotympanini)
from the Arid Regions of Central Australia
and Southwest Western Australia

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ABSTRACT. The genus *Arenopsaltria* is restricted to Australia, from which three species are described. Two, *A. fullo* and *A. pygmaea*, occur in coastal and subcoastal Western Australia; the third, *A. nubivena*, was thought to be restricted to the relatively small region from southeastern South Australia to northwestern Victoria, but is now known to occur much more widely into northeastern South Australia, southwestern Queensland, southern Northern Territory and with a possibly isolated population in southwestern Western Australia. The continuous buzzing calling song of *A. nubivena* is here documented from four well separated locations and is shown to be remarkably similar in temporal and other acoustic properties. The songs of *A. fullo* and *A. pygmaea* are also documented; both songs have a similar temporal structure, and both are distinct from the *A. nubivena* calling songs. MaxEnt modelling of the *A. nubivena* distribution can be linked by a climatic envelope in which the three most significant variables are precipitation variables, consistent with the currently known geographical distribution and emergence behaviour of this species in the warm to temperate margins of the arid zone, areas which experience sporadic and sometimes heavy summer rainfall events. Modelling of the estimated conditions at and since the Last Glacial Maximum (c. 22 ka), a period during which we expect to find the most significant contrast with the present-day distribution of *A. nubivena*, suggests an expanded distribution of this species during this period. Details of the geographic distributions will, however, be mediated by additional physical factors, such as dispersal barriers (e.g., the Nullarbor Plain), local interspecific interactions and other unsuitable habitats.

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The genus *Arenopsaltria* Ashton, 1921 is recorded only from Australia and currently has three described species. *Arenopsaltria fullo* (Walker, 1850), the type species of the genus, and *A. pygmaea* (Distant, 1904) are recorded from along coastal regions of Western Australia between the Murchison River in the north and the Margaret River south of Perth. The third species, *A. nubivena* (Walker, 1858), is so far documented only from southeastern South Australia to the far

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northwest of Victoria (Moulds, 1990, 2012). All three species occur in heathland, woodland with heath undergrowth and dry scrubland, all located in areas of sandy soils (Moulds, 1990).

This contribution documents a much wider distribution for *Arenopsaltria nubivena* based on examination of specimens in various collections, especially that of M. S. Moulds and University of Connecticut (Storrs, CT, USA) co-workers which is housed at Kuranda, Queensland. Based on colour and morphology (including multiple genitalic characters), specimens are identified from northeastern South Australia, southwestern Queensland, southern Northern Territory, and far southwestern Western Australia. This range clearly extends into the arid interior of central Australia and Western Australia, a classical Eyrean distribution, although in southwestern Western Australia trending to Bassian.

This paper also provides a redescription of *A. nubivena*, the original description dating to 1858. The male calling songs are documented for the first time, from audio recordings made from southwestern Queensland, Northern Territory and southwestern Western Australia. This is considered an integral aspect of current cicada studies, as the calling songs of most species are species-specific even when diagnostic morphological characters are few or absent (e.g., Popple, 2013). Songs are therefore important for confirming the identity of this species over the distances documented in this study. Representative songs of *A. fullo* and *A. pygmaea* are analysed for comparison. Finally, MaxEnt modelling is presented to explore the possible palaeobiogeographic distribution of this species during the late Pleistocene to Holocene period, that is, during the last c. 22 ka.

Materials and methods

Anatomical terminology. We follow the terminology of Moulds (2005, 2012) for general body shape and wing characters, Dugdale (1972) and Moulds (2005) for genitalia, Boer (1999) for opercula, and Simmons & Young (1978), Dugdale (1972) and Bennet-Clark (1977) for timbals. The long timbal ribs are referred to sequentially as ribs numbered 1 to 5, with rib 1 being the most posterior (adjacent to timbal plate). The higher classification adopted in this paper follows Moulds (2012). Measurements (in mm) are given as ranges and means (in parentheses) and include the largest and smallest specimens available. Head width is measured across the outer margins of the compound eyes; pronotum width is measured across the lateral margins (excluding ampliated lateral angles); and abdominal width is measured across the outer edges of the abdomen.

Abbreviations. *Institutions and collections—AE*, private collection of A. Ewart, Caloundra, Australia; *MSM*, private collection of M. S. Moulds and University of Connecticut co-workers housed at Kuranda, Australia; *QM*, Queensland Museum, Brisbane. *Collectors and general— Hwy*, highway; *NT*, Northern Territory; *Qld*, Queensland; *Rd*, road; *Rec*, recorded (= aural/electronic song recording); *RR*, repetition rate (pulses, syllables, macrosyllables); *SA*, South Australia; *sp*, species; *spec*, specimen; *PS*, prefix to Queensland Museum photo number; *WA*, Western Australia; *AE*, A. Ewart; *GM*, G. Monteith; *BJM*, B. J. Moulds; *MSM*, M. S. Moulds. *Morphological—BL*, total body length; *FWL*, fore wing length; *FWW*, fore wing width; *HW*, head width; *PW*, pronotum width; *AW*, abdomen width; *FWL/FWW*, fore wing length/width ratio.

Recordings. Recordings of *A. nubivena* were made *in situ* in the field with one of the following equipment combinations: AE used a Marantz PMD660 Solid State digital recorder in conjunction with either a Sennheiser model K6/ME66 microphone, or a parabola (Telinga model with Telinga PRO 5 "Classic" microphone), run in PCM mode at sampling rate of 48 kHz; DCM used a Marantz PMD660 or 670 recorder, with a Sennheiser ME-62 microphone and a Sony PBR-330 parabola. Filtering employed the time domain FIR procedure. Frequency analyses employed a 1024-point Fast Fourier Transform with Hamming window and 93.75% temporal resolution overlap, on 10–15 s segments of songs (including complete song phrases as appropriate). The recording of *A. fullo* was made in 1989 *in situ* in the field, utilising a Marantz CP430 cassette recorder in conjunction with Sennheiser microphone (ME 80/K3U). These had a linear response to near 15 kHz, and the cassette tapes were subsequently digitized through a 16-Bit Terratec sound card at a 44.1 kHz sampling frequency. All processing was undertaken with Avisoft SAS Lab Pro software.

Frequency analyses of the songs are displayed as amplitude spectra, and two parameters derived from these plots. One is the bandwidth, the second is the dominant frequency. These are used because the spectra show significant spreads of frequencies with multiple frequency peaks. The boundaries of the bandwidths are chosen so as to define a *dominant frequency envelope*, defined between the points where the main highest and lowest frequency peaks drop most rapidly towards the baseline, a procedure which does have a degree of potential operator bias. The frequency length of the envelope is taken as a measure of the bandwidth, and the dominant frequency is the mean frequency value of the envelope. Representative digital recordings will be deposited into the BioAcoustica Wildlife Database (http://www.bio.acousti.ca).

Systematics

Family Cicadidae Latreille, 1802
Subfamily Cicadinae Latreille, 1802
Tribe Cryptotympanini Handlirsch, 1925

Genus *Arenopsaltria* Ashton, 1921

Type species: *Arenopsaltria fullo* (Walker, 1850).

Included species: *fullo* (Walker, 1850); *nubivena* (Walker, 1858); and *pygmaea* (Distant, 1904).

Arenopsaltria nubivena (Walker)

Figs 1–9

Description. Male: Figs 1, 3A, 4.

Head. Width across compound eyes slightly less than across lateral margins of pronotum (excluding lateral angle of pronotal collar) and wider than mesonotum; vertex distinctly wider than supra-antennal plate, forming a broad and conspicuous extension to eyes; the eyes thus form the termination of the vertex, appearing as on a broad stalk extended away from the head when examined in dorsal view; vertex and frons pale to medium brown, slightly darker
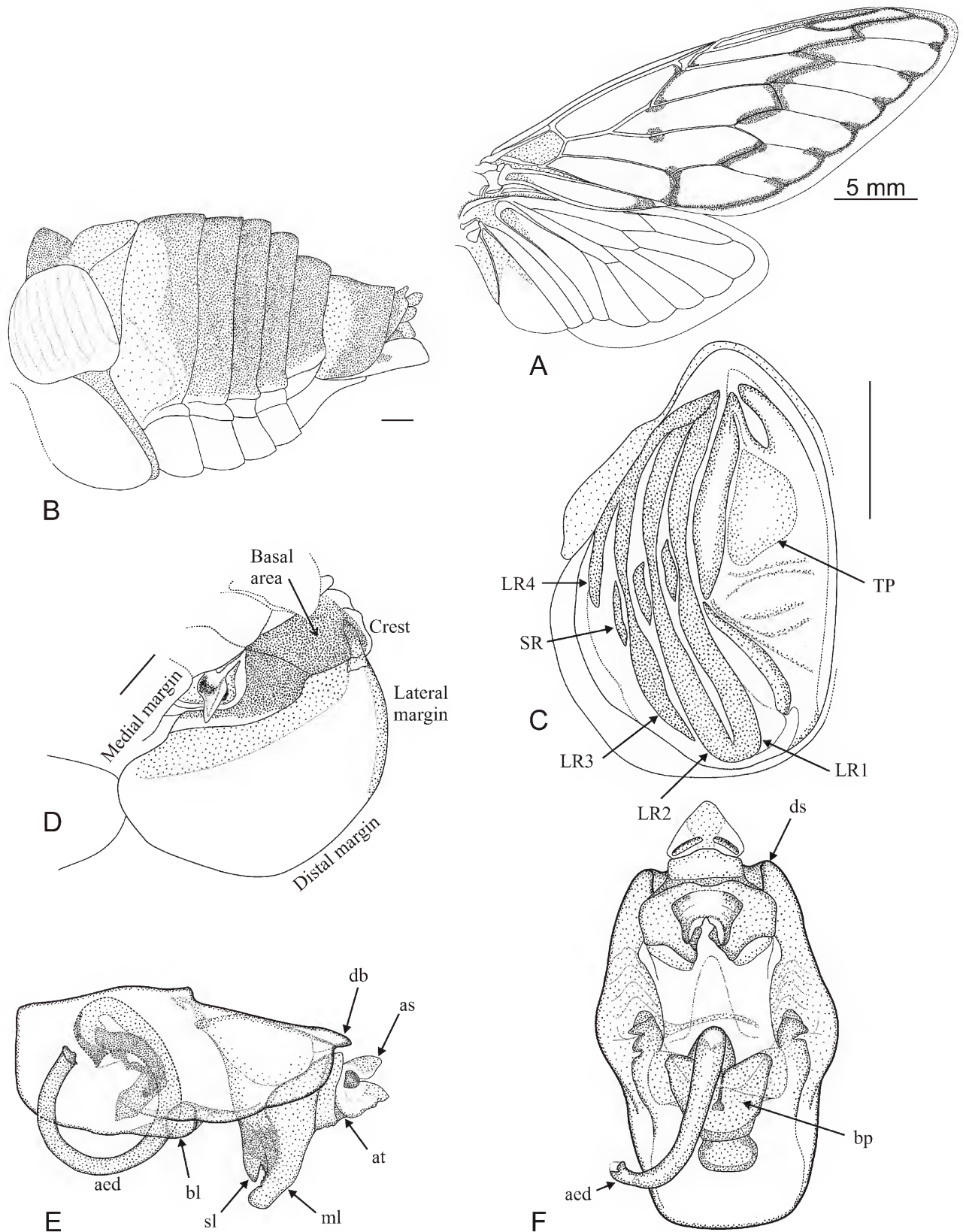
Figure 1. *Arenopsaltria nubivena*, 5.6 km west of Windorah, southwest Queeensland. *(A)* fore and hind wings; *(B)* lateral abdomen view; *(C)* left timbal, posterior margin at right, dorsal edge at top; *(D)* left opercula; *(E, F)* male pygofer and genitalia—*E*, lateral view; *F*, ventral view. Terminology for the opercula follows de Boer (1999; note that the crest is described fully by that author as "crest around distolateral corner of basal part of operculum"). Terminology for timbals: *LR1* to *LR4*, long ribs 1 to 4; *SR*, short (intercalary) ribs; *TP*, timbal plate. Terminology for pygofer: *aed,* aedeagus; *as*, anal styles; *at*, anal tube; *bl*, basal lobe of pygofer; *bp*, basal plate; *db*, dorsal beak; *ds*, distal shoulder; *md*, median lobe of uncus; *sl*, subapical lobe of uncus. Length of pygofer 3.8 mm. Scale bars 1 mm, except wings (5 mm).
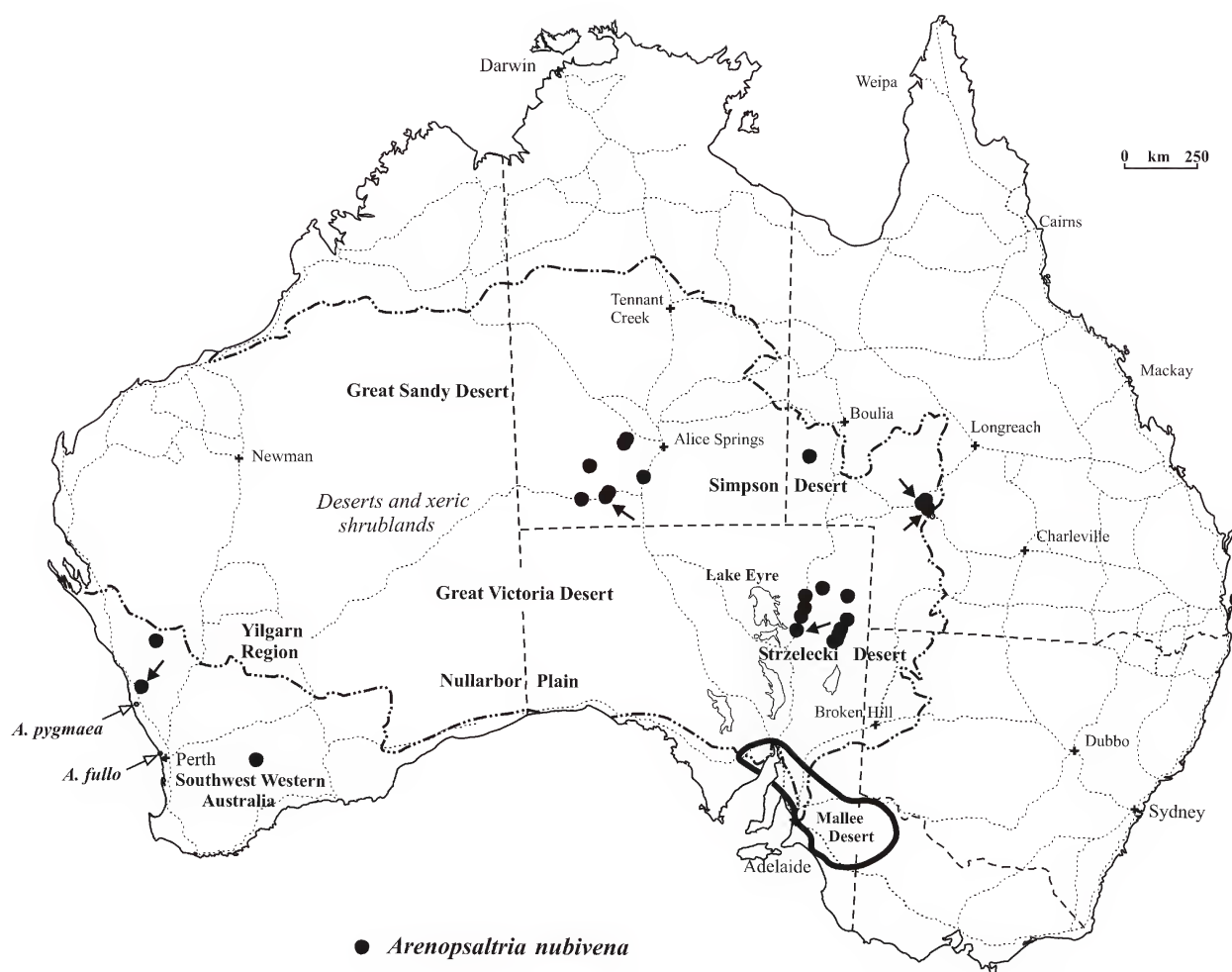
● *Arenopsaltria nubivena*

Figure 2. New distribution records for *Arenopsaltria nubivena*. Filled arrows indicate locations of audio recordings. The generalized distribution of *A. nubivena* in South Australia and northwestern Victoria, shown by the heavy circled line, is from Moulds (1990, 2012), and marks the known distribution prior to this work. The dotted lines are roads. The dashed lines are State boundaries. The dot-dash line shows the approximate boundary of the ecoregion which defines the dominance of deserts and xeric shrublands within inland Australia (National Reserve System map, published by Australian Government). The filled arrows mark the locations of the audio recordings of *A. nubivena* illustrated in this paper. The hollow arrows show the locations of the audio recordings of *A. fullo* and *A. pygmaea*. The general locations of the major dunefields and other relevant areas noted in the text are labelled.

medially; supra-antennal plate pale brown; ocelli pale red; length between lateral ocelli much less than between ocelli and eyes; postclypeus somewhat bulbous in anterior view, flattened in dorsal view, and gently rounded in lateral profile, pale brown, slightly darker along transverse ridges; head and the transverse ridges of postclypeus covered with very short golden pubescence; anteclypeus pale brown, covered by short golden pubescence laterally; rostrum brown, darker apically, reaching hind coxae; gena and mandibular plate pale brown, covered by short golden pubescence; antennae dark brown.

Thorax. Pronotum: width at dorsal midline much less than diameter of eyes; paranota slightly ampliate, becoming strongly ampliate on lateral angle of pronotal collar; paranota showing slight but distinct serration, no mid lateral tooth; conspicuous broad sandy-brown central fascia, broadest at anterior and posterior termination, with narrow black margin that partially extends along paramedian fissures; remaining pronotal colouration pale brown, with small black spots on the anterior part of the lateral fissures.

Mesonotum: submedian sigilla variably deep brown, grading to paler brown medially, bordered by prominent black to deep brown parapsidal sutures; lateral sigilla dark brown, not sharply defined, grading into the generally paler brown of the enclosing mesonotum; cruciform elevation wider than long, pale brown, slightly darker along anterior arms; areas between lateral cruciform elevation arms dark brown to black, grading into scutal depressions, these areas covered by prominent white pubescence; epimeral lobe reaching operculum; surface of mesonotum uneven; ridges between wing grooves sandy brown, black within grooves; metanotum concealed on dorsal midline.

Wings (Fig. 1A). Fore wing: Hyaline, with 8, very rarely 7, apical cells; no subapical cells; ulnar cells longer than apical cells, with ulnar cell 3 angled to radial cell; radial cell shorter than ulnar cells; basal cell broad, mostly filled by brown infuscation; height of costal vein comparable to R+Sc vein; costal plus R+Sc veins almost parallel to node; pterostigma present and darkly infuscated especially along anterior margin; vein CuA very weakly bowed to cubital cell,
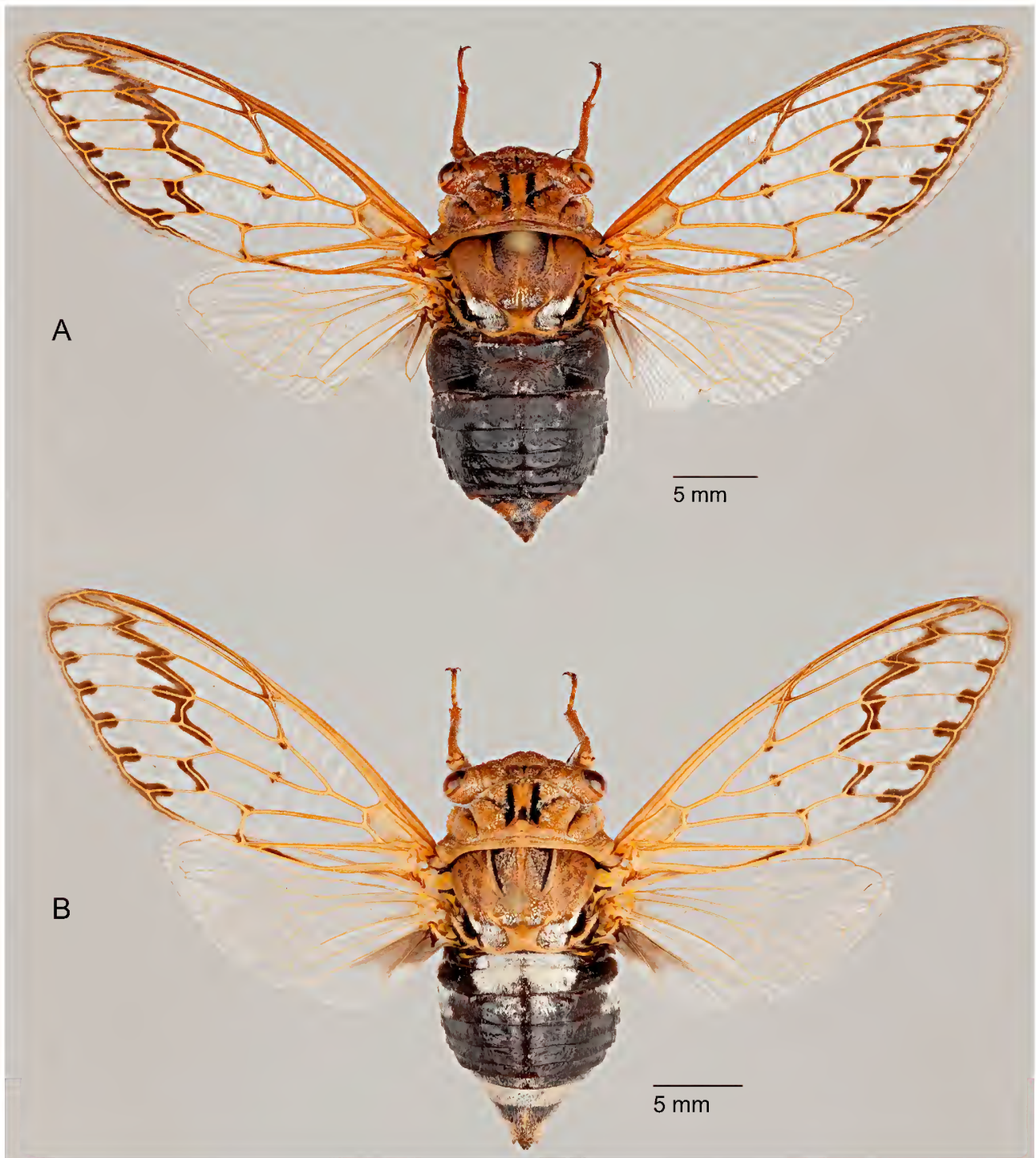
Figure 3. *Arenopsaltria nubivena* (Walker); *(A)* male, Queensland Museum reference QMT196193, body length 22.6 mm; *(B)* female, QMT196194, body length 21.7 mm. Both specimens from Pulchera Waterhole, Mulligan River, Ethabuka Reserve, southwest Queensland.

with the medial cell of similar width, although larger in area; cubital cell occasionally divided by an extra vein; veins M and CuA widely separated at their intersection with basal cell; vein RA_1 almost parallel to Sc for its length; vein CuA_1 divided by crossvein m-cu, with both segments of similar length; veins CuP and 1A fused for most of their lengths; very distinctive areas of dark black to brown infuscation overlying veins at bases of apical cells 2–6, weakly on and around apical cell 1, also adjacent to the ambient veins, in part proximally along veins between apical cells, distally between the 3A and 2A veins near their junctions with CuA_2, on the join between CuA_2–CuA_1 veins at the nodal line intersection on vein M_{3+4}, and apically along vein M between its joins with the M_{1+2} and RP veins; outer wing margin clearly present for entire length; basal membrane colourless to pale brown; veins predominantly pale brown. Hind wing: 6 apical cells (very rarely 5 on one wing); no infuscation on or along ambient vein; width of 1st cubital cell at distal end variable, usually

Figure 4. *Arenopsaltria nubivena* (Walker), male holotype, body length 21.4 mm, held in the British Museum of Natural History.

less than that of 2nd cubital cell; anal lobe broad with vein 3A curved, separated from wing margin; veins M and RP fused basally; anal cells 2 and 3 with basal grey infuscation, fading out distally; veins pale sandy-brown, tending darker basally.

Legs: Two erect spines on fore femora; fore and mid coxae and trochanters pale brown, broad anterior dark brown fasciae on ventral and anterior faces of coxae, and 2 to 3 smaller dark brown fasciae on anterior trochanter faces; fore and mid femora, tibiae and tarsi pale to medium brown, grading to black on claws; hind coxae pale brown with extensive dark brown on anterior and dorsal faces; hind femora with pale and dark brown longitudinal fasciae; hind tibiae medium brown with 6 tibial spurs, and clusters of very small spines at distal end of tibiae (tibial comb and thumb of tibial comb); tarsi medium brown, grading to black on claws.

Timbal (Fig. 1C). Completely covered by a very rigid black timbal cover, not bulbous, tightly fused to tergites 1 and 2, covered with gently curved, near vertical striations produced by micro-ridging of the surface; removal of the cover shows the timbal to contain four long timbal ribs; ribs 3 and 4 fused dorsally to basal spur; ribs 1 and 2 juxtaposed dorsally to (but not fused to) basal spur, these two ribs fused ventrally; three very prominent intercalary ribs; an elongated ridge located on the timbal plate posteriorly to long rib 4 suggesting a possible additional unconnected rib, its morphological status uncertain; a narrow basal dome lies parallel to, and dorsoposteriorly to, long rib 4; anterodorsal area of timbal plate filled by a shallow and well-defined ridge; posterior area of timbal plate contains gentle ridges and a shallow domed structure.

Opercula (Fig. 1D). Completely covers timbal cavity, just overlapping tergite 2; broadly ovoid in outline; well developed suture visible, marking the fused junction between the anterior remnant of the epimeron and the main posterior segment of operculum; the area anterior to the suture is black; posterior and lateral to suture the colour ranges between dark brown and pale brown along distal and lateral margins; posterior area immediately adjacent to suture slopes

downwards (as viewed ventrally) towards suture; meracantha spike overlaps opercula plate.

Abdomen (Fig. 1B). Overall form short and very broad; in cross-section, tergites strongly convex, epipleurites reflexed ventrally from junction with tergites; tergites 2 and 3 wide, together making up nearly half of abdominal length; tergites 1 and 2 black, covered medially by dense, very short silvery pubescence and patches of waxy exudation; tergites 3–7 shiny black, grading to brown on posteroventral margin of tergite 7, with localized wax patches on especially tergite 3; tergite 8 deep brown to black along anterior margin, also as a narrow fascia along dorsal midline, and as a narrow band along posterior dorsal and lateral margins; otherwise sandy-brown. Sternite II dominantly black; sternite III pale brown; sternite IV black medially, grading to brown laterally; sternites V to VII brown, paler towards sternite VII; sternite VIII pale yellow-brown; sternite IX brown medially, sandy brown laterally; sternites all covered by very short silvery pubescence.

Genitalia (Fig. 1E, F). Pygofer black to dark brown anterodorsally, remainder pale sandy brown; distal shoulders broad, rounded in lateral view; upper lobes undeveloped; lower lobes clearly developed, distally rounded in lateral view, somewhat irregular in ventral outline; dorsal beak small but clearly developed, part of chitinized pygofer; uncus undivided, with enlarged median lobe which is somewhat finger-like in lateral view, widest between subapical rounded lobes, and apically tending to be bilobed; claspers absent. Aedeagus with basal plate in lateral view sharply angled to nearly 180°; in dorsal view with short apical arms, the base broad and long, deeply furrowed along midline; basal portion of basal plate directed forwards, away from thecal shaft; ventral rib fused with basal plate; junction between theca and basal plate fused and rigid; thecal shaft recurved to as much as 360°; pseudoparameres absent; thecal apex chitinized; no subapical cerci; no flabellum.

Female: (Fig. 3B).

Head, pronotum and mesonotum mostly very similar in colours and markings to male, in some specimens the colour is predominantly medium to dark brown rather than paler brown; legs as in male, although again noting the darker brown colouration of some specimens; wings with identical structures and markings to male.

Abdomen, tergite 1 narrow, mostly black, tending paler along posterior margin; tergite 2 slightly wider along dorsal midline than tergites 3–7, with extensive short silvery pubescence medially, otherwise shiny black; tergite 3 predominantly shiny black, with pale brown area anteroventrally; tergites 4–7 predominantly shiny black, with brown on ventral reflexed areas; tergite 8 deep brown to black along entire anterior area, with the remainder sandy brown, the boundary between these two colour zones irregular; tergite 9 with wide irregular black dorsal to sub-medial colouration, dorsally forming a broad midline extending full width of tergite, interrupted by a narrow medial longitudinal sandy brown fascia; remainder of tergite 9 sandy brown to brown, with diffuse brown lateral stigma; sternite I dark brown to black; sternites II brown; sternites III to VII dark brown; ovipositor sheath black, in lateral view anteriorly lying subparallel to sloping tergite margin, distally extending 0.7–1.3 mm beyond the apex of the tergite.

Measurements. Table 1 compares measurements from various locations. These data show a close coherence of the morphological dimensions across the specimens representing the widely separated populations sampled.

Distribution, habitat and behaviour (Fig. 2). The previously recorded distribution of this species (Moulds, 1990, 2012) extends from 40 km west of Kimba at the top of Eyre Peninsula, southeastern South Australia, northeastwards to Hattah Lakes and Wyperfield National Parks, in the far north-west of Victoria. The following are additional locations: QUEENSLAND: 1♂, QMT196193, Pulchera Waterhole, Mulligan River, 7 Nov 2010, W.C.Q., 23°55.863'S 138°38.117'E, A.J. Emmott. In cane grass, on dune, Ethabuka Reserve. Photographed Specimen. 1♀, QMT196194, Pulchera Waterhole, Mulligan River, 7 Nov 2010, W.C.Q., 23°55.863'S 138°38.117'E, A.J. Emmott. In cane grass, on dune, Ethabuka Reserve. Photographed Specimen; 10♂, 4♀, Pulchera Waterhole, Mulligan River, as previously. **(QM)**. 1♂, 2 miles W. of Windorah, southwestern Qld., 10.iv.1971, G.B. Monteith **(UQIC, QM)**. 1♂, 1♀, Sand dune crest, c.5.6 km northwest of Windorah, southwest Qld., on *Crotalaria eremaea*, A.E., 4.ii.2010, 25°23.47'S 142°36.82'E, male audio recorded; 1♂, sand dune crest, c.5.7 km northwest of Windorah, southwest Qld., on *Grevillea stenobotrya*, A.E., 6.ii.2010, 25°23.40'S 142°36.65'E **(AE)**. 1♀, Ourdel Stn., nr. Windorah, southwest Qld. in burrow on dune, 9.iii.2007, S. Wilson; 11♂, 2♀, 09.AU.QL.DUN.01-02, 27 km southeast of Windorah, eastern margin of Cooper Creek floodplain, southwest Qld, 2.ii.2009, 25.4811°S 142.832°E, K. Hill, D. Marshall, male audio recorded. **(MSM)**. NORTHERN TERRITORY: 29♂, 9♀, Finke R. crossing, 120 km SW of Alice Springs, N.T., 20.i.1984, M.S. & B.J. Moulds; 191♂, 82♀, Finke River near Glen Helen Gorge, N.T., 28.i.1984, M.S. & B.J. Moulds; 5♂,

Ormiston Gorge, 130 km W. of Alice Springs, N.T., 29.i.1984, M.S. & B.J. Moulds; 4♂, 1♀, Kings Canyon, George Gill Rg., N.T., 31.i.1984, M.S. & B.J. Moulds; 3♂, 1♀, 29 km NE of Curtin Springs Hstd., E. of Ayers Rock, N.T., 2.ii.1984, M.S. & B.J. Moulds; 3♂, 1♀, 28 km E. of Curtin Springs Hstd., E. of Ayers Rock, N.T., 6.ii.1984, M.S. & B.J. Moulds; 1♂, 10.AU.NT.LSA.02, c.105 km ESE Yulara, Ayers Rock Resort, Lasseter Hwy, 1.ii.2010, 25.2455°S 131.992°E, K. Hill, D. Marshall, male audio recorded; Aural record: 1♂, 10.AU.NT.LSB., c.25 km ESE of Yulara, Ayers Rock Resort, Lasseter Hwy, 2.ii.2010, 25.2202°S 131.23°E, K. Hill, D. Marshall; c.105 km ESE Yulara, Ayers Rock Resort, Lasseter Hwy, 1.ii.2010, 25.2455°S 131.992°E, K. Hill, D. Marshall, male audio recorded (10.AU.NT.LSA.02); 1♂ aural record. **(MSM)**. SOUTH AUSTRALIA: 3♂, NNW of Tingatingana Ck., Strzelecki Creek, S.A., 23.i.1976, in sand dunes, 28°44'S 140°09'E, M.S. & B.J. Moulds; 14♂, near Moomba Gas Field, S.A., 24.i.1976, in sand dunes, approx. 28°05'S 140°13'E, M.S. & B.J. Moulds; 1♂, 12km SSW of Mungerunn (Mungerannie), [Birdsville Track], S.A., 28°7'22"S 138°39'23"E, 4.iii.2003, stoney desert, mu005; 6♂, 15.AU.SA.CCK, Cooper Creek, main channel on Birdsville Track, 30.i.2015, 28°35.707'S 138°42.902'E, D. Marshall; 1♂, 15.AU.SA.CCM, 17 km S of Cooper Ck main channel, Birdsville Track, 30.i.2015, audio recorded, 28°43.534'S 138°37.394'E, D. Marshall; 2♂, 15.AU.SA.CCN, 72 km S of Cooper Ck main channel, Birdsville Track, 30.i.2015, audio recorded, 29°10.731'S 138°24.357'E, D. Marshall; 1♂, Strzelecki Track, c. 8 km ENE of Arkaroola Rd jct, 31.i.2015, audio recorded, 29°31.211'S 139°53.484'E, D. Marshall; 6♂, 3♀, 15.AU.SA.SZA, Strzelecki Track, c.17 km ENE of Arkaroola Rd jct, 31.i.2015, audio recorded, 29°28.081'S 139°57.133'E, D. Marshall; 1♂ audio recorded, Strzelecki Track, c.32 km NE of Arkaroola Rd jct, 31.i.2015, 29°20.511'S 140°01.484'E, D. Marshall; 1♂ audio recorded, Strzelecki Track, 31 km S of Strzelecki Crossing, 1.ii.2015, 29°12.900'S 140°04.463'E, D. Marshall. **(MSM)**. 1♂ photographed, Cooper Ck floodplain, Beach Energy Callawonga Camp, approx 87 km WNW of Moomba, 27.1.2015, 27°55.6214'S 129°20.4354' E, Jan Scott. **(JS)**. WESTERN AUSTRALIA: 1♂, East Hyden, W.A., 29.i.1985, S. Lamond; 1♂, 35 km E of Pindar, W.A., 11.ii.2001, M. Powell, D. Knowles; 1♂, 1♀, AU.WA.EEN, 18 km E of Eneabba, 21.i.2003, audio recorded, 29°45.404'S 115°25.939'E, Moulds, Marshall, Vanderpool **(MSM)**.

A species with a preference for the arid regions of Central Australia, including southwest Queensland, southeastern and northeastern South Australia, northwestern Victoria, and semi-arid shrubland regions of southwestern Western Australia. It inhabits dense patches of low to medium height vegetation on sandy soils, very commonly on sand dunes, sometimes on dunes quite isolated from more extensive dune fields, and frequently in general proximity to ephemeral creeks and lakes. Vegetation on which this species has been found includes *Crotalaria eremaea* (Rattlepod), *Grevillea stenobotrya* (Sandhill Spider-flower), and *Zygochloa paradoxa* (Sandhill Canegrass). It is a relatively sedentary species, tending to remain for extended periods in the same general location. Following heavy summer rains, records indicate that it emerges in relatively large numbers.

Table 1. *Arenopsaltria nubivena* measurements (mm) from multiple locations in northeastern South Australia, southern Queensland, and southwestern Western Australia. *AW*, abdomen maximum width; *FWB*, maximum width forewing; *FWL*, length forewing; *HW*, head width across eyes; *PW*, pronotum width excluding ampliated collar; *TBL*, total body length; *n*, number of specimens measured.

location	n	TBL	FWL	FWW	HW	PW	AW	FWL/FWW	AW/HW
Southern Populations									
40 km W Kimba, southeastern SA plus northwestern Victoria	♂ 13	22.1 (19.4–23.4)	25.4 (22.2–28.8)	9.5 (8.6–10.2)	9.0 (8.1–9.6)	8.2 (7.2–8.7)	9.5 (8.5–10.2)	2.67 (2.59–2.83)	1.06
	♀ 2	22.8 (22.6–23.0)	27.4 (26.0–28.8)	10.0 (9.6–10.4)	9.5 (9.3–9.7)	8.7 (8.3–9.1)	9.9 (9.5–10.2)	2.74 (2.71–2.77)	1.04
Northern Populations									
southwestern Qld, Windorah and Ethabuka areas	♂ 20	22.0 (20.0–24.3)	26.2 (24.0–27.9)	9.9 (9.1–10.5)	9.0 (8.0–9.7)	8.6 (7.9–9.2)	10.1 (9.0–10.9)	2.65 (2.47–2.86)	1.12
	♀ 7	22.8 (21.7–24.1)	26.9 (25.3–28.7)	10.1 (9.3–10.8)	9.2 (8.6–9.7)	8.7 (8.1–9.3)	10.0 (9.3–10.5)	2.66 (2.58–2.85)	1.09
NT, Kings Canyon, George Gill Range	♂ 3	23.2 (22.9–23.4)	26.8 (26.6–27.0)	10.1 (9.9–10.4)	9.0 (8.9–9.1)	8.5 (8.1–9.0)	9.9 (9.8–10.0)	2.65 (2.55–2.73)	1.10
	♀ 1	22.8	28.0	9.7	9.3	8.7	9.3	2.89	1.00
NT, Finke River, 120 km SW Alice Springs	♂ 6	20.8 (20.0–21.6)	25.9 (25.2–26.9)	9.9 (9.5–10.1)	8.8 (8.6–9.1)	8.8 (8.4–9.0)	9.8 (9.2–10.2)	2.62 (2.55–2.74)	1.11
	♀ 5	22.0 (20.5–24.1)	28.2 (27.4–29.7)	10.4 (10.0–11.2)	9.2 (8.9–9.6)	9.3 (8.8–9.9)	10.4 (9.9–11.3)	2.71 (2.59–2.86)	1.13
NT, Finke River nr Glen Helen Gorge	♂ 10	20.9 (19.0–22.2)	25.8 (24.2–27.4)	9.4 (8.4–10.8)	8.8 (8.4–9.2)	8.6 (7.9–9.1)	9.3 (8.5–9.9)	2.74 (2.61–2.93)	1.06
	♀ 10	21.7 (19.5–24.4)	26.4 (24.8–28.1)	9.9 (9.0–10.4)	8.9 (8.0–9.4)	8.9 (8.4–9.2)	9.5 (9.1–10.8)	2.67 (2.54–2.76)	1.07
northeastern SA, Moomba and Strzelecki and Birdsville Tracks[a]	♂ 23	23.1 (20.6–24.5)	27.3 (25.8–28.4)	10.5 (9.7–11.4)	9.5 (8.8–10.2)	9.3 (8.3–10.6)	10.6 (9.4–11.3)	2.59 (2.41–2.74)	1.11
	♀ 4	23.6 (22.9–24.5)	27.9 (27.3–28.2)	11.2 (10.9–11.4)	9.7 (9.1–10.1)	9.4 (9.0–9.7)	10.7 (10.4–11.0)	2.49 (2.46–2.51)	1.10
Western Australian Populations									
18 km E of Eneabba	♂ 1	22.7	26.2	10.7	9.2	7.8	9.4	2.45	1.02
	♀ 1	24.5	27.4	10.9	9.8	8.1	9.8	2.51	1.00

[a] Includes specimens from seven localities.

Table 2. *Arenopsaltria nubivena* calling songs—comparative song parameter data from multiple locations. All data presented as means, ranges of values in square brackets; *ms*, milliseconds; *n*, number of measurements; *RR*, repetition rates.

	southwest Qld, 5.6 km W Windorah	southwest Qld, 19 km ESE Windorah	northeast SA, Strzelecki and Birdsville Tracks[a]	southern NT, 105 km ESE Yulara	Western Australia, 18 km E Eneabba
macrosyllable RR —3 syllables	192 Hz [179–217] early in song, to 263 Hz [227–294] for main song (n=30)	222 Hz [196–256] main song, to 200 Hz [189–227] at end of song (n = 37)	241 Hz [211–276] (n = 21)	244 Hz [227–256] (n=11)	222 Hz [213–238] (n=19)
macrosyllable durations —3 syllables	4.2 [4.0–4.5] early in song to 3.4 [3.0–3.9] for main song (n = 57)	4.0 [3.4–4.6] for main song to 3.6 [3.4–4.3] at end of song (n = 39)	3.4 [2.9–3.9] (n = 20)	3.6 [3.4–3.9] (n = 124)	3.7 [3.4–4.0] (n = 19)
macrosyllable RR —6 syllables	95 Hz [85–105] early in song to 132 Hz [125–137] for main song (n=14)	111 Hz [102–116] for main song (n = 9)	127 Hz (123–132) (n = 21)	—	120 Hz [108–125] (n=36)
macrosyllable durations —6 syllables	9.1 [8.4–9.7] early in song to 7.1 [6.7–7.6] for main song (n = 32)	8.4 [7.7–9.2] for main song (n = 9)	7.0 [6.5–7.7] (n = 22)	—	7.5 [7.1–8.6] (n = 36)
syllable RR within macrosyllables	746 Hz [546–1000] (n = 77)	714 Hz [526–769] for main song to 667 Hz [526–769] at end of song (n = 62)	810 Hz (641–990) (n=154)	833 Hz [769–909] (n=22)	714 Hz [625–769] (n=55)
gaps between 3-syllable macrosyllables	0.8 [0.4–1.5] early in song to 1.3 [1.2–1.5] (n = 18)	0.7 [0.3–1.5] for main song, 1.6 [0.7–2.1] at end of song (n = 23)	0.7 [0.5–1.0] (n = 19)	1.7 [1.5–2.0] (n = 11)	0.8 [0.6–0.9] (n = 30)
gaps between 6-syllable macrosyllables	0.9 [0.5–1.5] early in song to 1.5 [1.3–1.8] for main song (n = 16)	0.8 [0.4–1.5] (n = 15)	1.0 [0.7–1.4] (n = 25)	—	0.8 [0.7–1.0] (n = 36)
dominant frequency (kHz)	8.2	8.1	7.4–7.8	8.1	7.7–8.0
bandwidth (kHz)	3.1	3.0	3.1–4.1	3.4	2.3–2.4

[a] Based on recordings from four locations (see text).

Table 3. Comparison of calling song parameters between *Arenopsaltria fullo*, *A. pygmaea* and *A. nubivena*. Data presented as mean values ± 1σ; ranges in square brackets; *n*, number of measurements; equivalent values in *ms* (milliseconds), in parentheses.

variable	*A. fullo* Mullaloo Beach North Perth	*A. pygmaea* 14 km NE of Jurien, N of Perth	*A. nubivena* summary of Table 2 data
macrosyllable durations (ms)	22.0±0.9 (n=63) [20.8–23.9]	21.6±3.2 (n=117) [15.5–26.9]	3.6 (3 syllables) [2.9–4.6] (n=259) 7.3 (6 syllables) [6.5–9.2] (n=99)
macrosyllable repetition rates (Hz)	34.8±0.7 (n=62) [32.9–35.7] (≈28.8 ms)	30.9±3.8 (n=118) [25.6–37.9] (≈32.4 ms)	238 (3 syllables) [196–294] (n=113) 123 (6 syllables) [102–137] (n=80)
mean syllable repetition rates within macrosyllables (Hz)	463±8 (n=49) [437–473] (≈2.2 ms)	725±65 (n=56) [613–813] (≈1.4 ms)	767 (n=370) [526–1000] (≈1.3 ms)
syllable doublets—repetition rates (Hz)[c]			
(a) syllable 1 to syllable 2 within doublets (Hz)	549±68 (n=70) [442–775] (≈1.8 ms)	—	—
(b) syllable 2 to syllable 1 of following doublet (Hz)	404±56 (n=70) [311–599] (≈2.5 ms)	—	—
number of syllables per macrosyllable	10–11	11–18	3 and/or 6
dominant frequency (kHz)	6.9	9.8	7.4–8.2
bandwidth (kHz)	2.8	2.7	2.3–4.1

[c] In *Arenopsaltria fullo*, the syllables predominantly occur in distinct doublets within each macrosyllable.

5.6 km W of Windorah, southwest Queensland

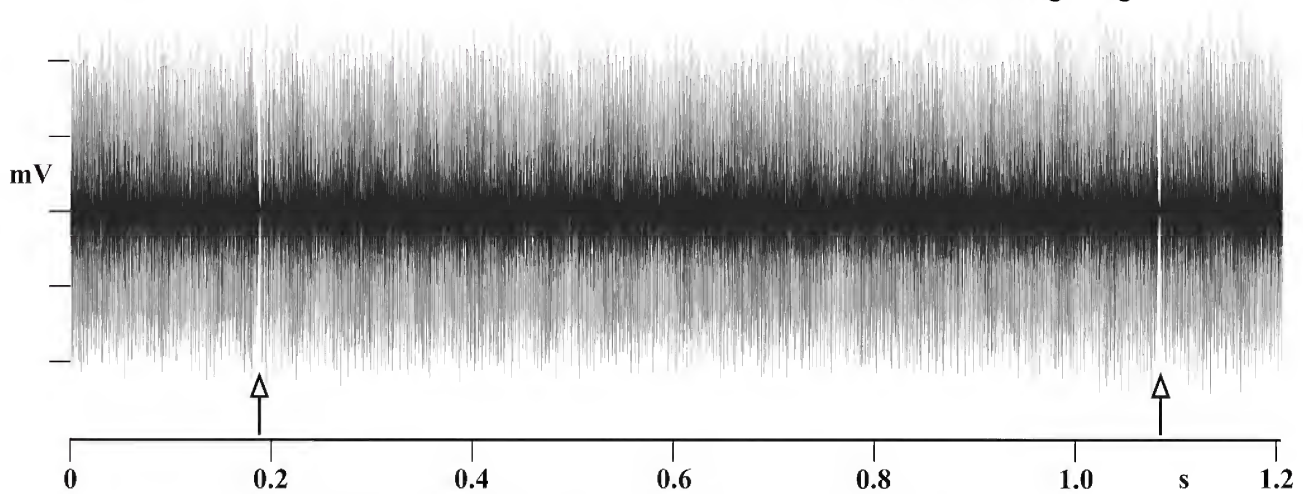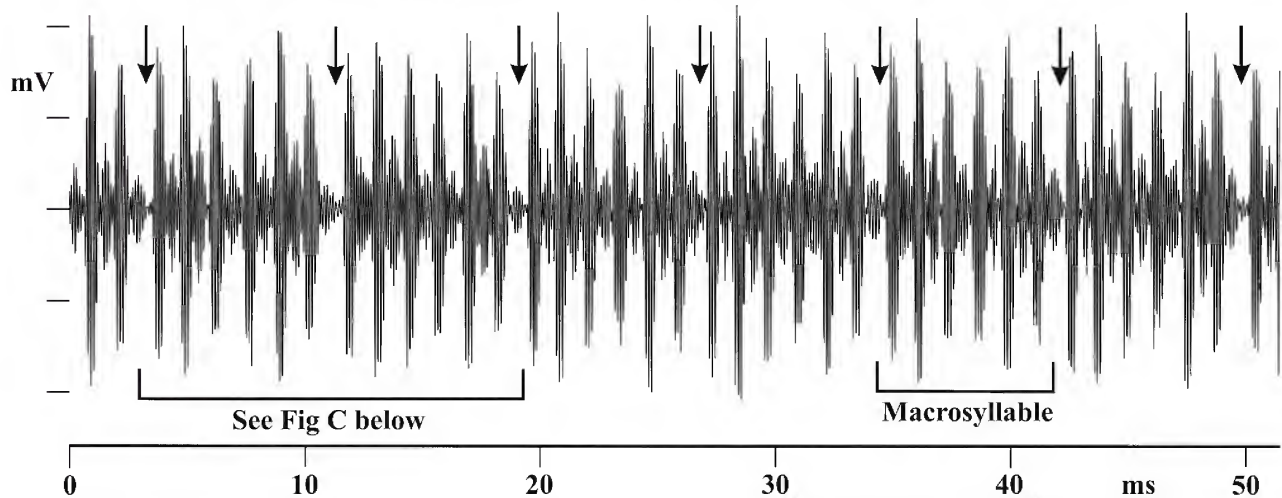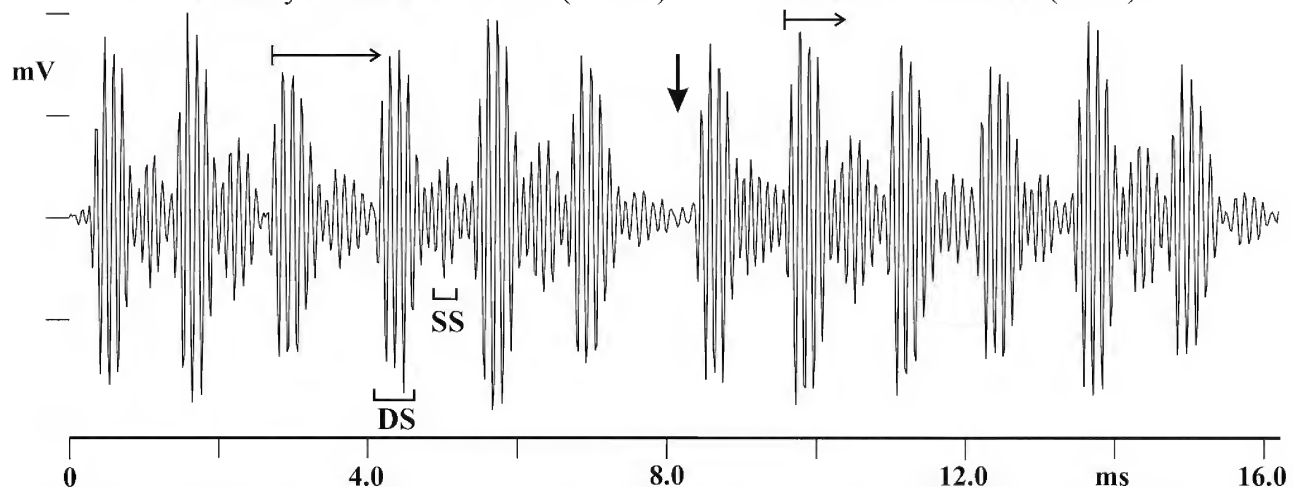A   continuous buzzing song

B   macrosyllable RR 128 Hz (7.8 ms), mean durations 7.4 ms

See Fig C below   **Macrosyllable**

C   mean syllable RR = 746 Hz (1.3 ms)   dominant to secondary syllable
                                            durations = 0.76 ms (mean)

SS

DS

Figure 5. *Arenopsaltria nubivena*, waveform plots of calling songs from 5.6 km west of Windorah, southwest Queensland; *(A)* general view showing the relatively uniform, continuous buzzing song, but showing two short breaks (marked by hollow arrows); *(B)* time expanded segment of calling song showing the repeated macrosyllables, each with six dominant syllables, the arrows defining the limits of the individual macrosyllables; *(C)* higher resolution waveform plot of two macrosyllables, the filled arrow marking the boundary between the macrosyllables. The six dominant syllables (DS) each comprise 5 to 7 high amplitude carrier wave pulses. The time intervals between the dominant and secondary syllables (SS) comprise lower amplitude background pulses, variably frequency modulated; the horizontal arrows define the syllable repetition rates (RR) and the intra-syllable durations between the dominant and secondary syllables. Field recordings, filtered to 1 kHz.

Calling songs

Figs 5–9, Table 2

Song terminology: The following terminology is used in this paper to describe the cicada songs. The terms pulse, syllable, macrosyllable, and echeme are the main technical terms used. In cicadas which emit calling songs with relatively low to moderate frequencies (approx. <10 kHz), the carrier pulses are resolved in higher resolution audio recordings when these are examined in waveform and envelope plots which allow the carrier pulses to be readily seen. The resolution of these, however, can complicate song terminology in the more complex calling songs, specifically in regard to the definition of carrier pulses and syllables. Sueur (2002), for example, illustrates songs in which strongly developed bursts of acoustic energy are referred to as "pulses", yet clearly comprise multiple smaller pulses which he refers to as "elementary oscillations". In this paper, we define *pulses* (the "elementary oscillations" of Sueur, 2002) as the very short and sharp bursts of sound energy, commonly between 0.1 to 0.2 ms in duration, one or more of which result from a single click of one timbal or the simultaneous clicking of both timbals, and in this paper, we equate these with the carrier pulses of the *Arenopsaltria* songs. Individual pulses involve movement contraction and then expansion of the timbal muscles, leading to inward then outward movement of the timbal ribs, the exact configuration of a complete movement being dependent on the species (e.g., Fleming, 1975). Multiple pulses stereotypically are grouped into natural, coherent higher amplitude bursts of acoustic energy, which we term syllables. These comprise the higher amplitude dominant syllables and weaker secondary syllables (see Figs 5 and 8). In the example of the *A. nubivena* songs, there are 5 to 7 pulses per dominant syllable. The pulses thus represent multiple sound waves with a range of sound frequencies characteristic of the species, and together define the composition of the syllables, background noise and reverberations generated during the sound emissions. This terminology is consistent with that used by Fleming (1975) and Young (1972).

Macrosyllables are coherent sets of multiple syllables, comprising distinct and measureable units. *Echemes* result from the extended merging or near coalescence of sets of macrosyllables, typically forming a continuous buzzing element.

Calling song of *Arenopsaltria nubivena*

The calling songs are continuous, somewhat monotonous and relatively high pitched "buzzing" (Fig. 5A) sounds, which may last up to at least four minutes without significant interruption. Within these buzzing sequences, however, are very small breaks, 1.4 to 3.6 ms in duration; two such breaks are illustrated in Fig. 5A. The spacing between these breaks is erratic, varying from <0.1 to >60 seconds, with most occurring only within relatively short segments of the songs.

The selected waveforms shown are from five locations, two from dune systems in far SW Queensland (Figs 5, 6), one from a dune 105 km ESE of Yulara, southern Northern Territory (Fig. 7A), one from shrubland 18 km E of Eneabba, southwestern Western Australia (Fig. 7B, C), and one from 72 km south of Cooper Creek crossing, Birdsville Track, Strzelecki Desert Reserve, northeastern South Australia (Fig. 7D). Measured song parameters are summarized in

Table 2. The song recorded from 5.6 km west of Windorah, southwestern Queensland, as seen in time expanded plots (Fig. 5B, C), comprises repeated macrosyllables, each comprising six high amplitude syllables. Syllable durations (Table 2, main song) range between 8.4–9.7 ms, with mean repetition rates of 132/s. The earliest song segments exhibit the longer syllable durations and lower repetition rates, presumably the "warming-up" phase. Syllable repetition rates (Fig. 5C) in each macrosyllable range between 680–1000/s.

Although six high amplitude syllables per macrosyllable is most typical of this song, some incipient splitting of the macrosyllables into two macrosyllables (each with three syllables) is observed. As seen in Figs 5C and 6A, the individual high amplitude (dominant) syllables are usually followed by lower amplitude secondary syllables, the duration between them defined as the intra-syllable duration. The mean intra-syllable duration measured on multiple recordings is 0.76 ms (n = 55, range 0.41–0.95 ms). The dominant syllables comprise 5 to 7 pulses, the secondary syllables each comprise 3 to 4 pulses, these forming the main acoustic components of the songs. Further discussion of these is given below (see Fig. 8).

Time expanded waveforms of the song from 19 km east-southeast of Windorah (Fig. 6A) show the clear division of the song into macrosyllables, these predominantly with three syllables, with a mean macrosyllable duration of 4.0 ms and mean repetition rate of 222 Hz. Nevertheless, some song segments (Fig. 6B) exhibit macrosyllables with six syllables, the initial syllable being relatively high amplitude, with a mean macrosyllable duration of 8.4 ms (repetition rate: 111 Hz). An additional significant change in the macrosyllable structure is observed at the end of an extended buzzing echeme (Fig. 6C), marked by the much reduced amplitude of the third syllable in each macrosyllable. That this third syllable is still a separate syllable is confirmed by the inter-syllable durations, the mean values between syllables 1 and 2 being 1.4 ms and between syllables 2 and 3 being 1.7 ms. Note is made of the gap of 17 ms at the end of this same song (Fig. 6C), followed by a short isolated macrosyllable comprising two syllables. In cicadas belonging to the Cicadettinae, comparable gaps have been noted to provide a marker for female wing-flick responses (e.g., Gwynne, 1987; Bailey, 2003; Marshall & Hill, 2009), but this has not so far been confirmed in the Cicadinae and we are unaware of any other evidence suggesting the existence of acoustic duets in *Arenopsaltria*.

The waveform plot of the song from the southern Northern Territory (Fig. 7A) is characterized by macrosyllables of three syllables only, with a mean macrosyllable duration of 3.6 ms. The songs from Western Australia exhibit comparable phrase structures to those described above, mostly with six main syllables per macrosyllable, but in places showing a transition from six to three syllables (Fig. 7B, C). The mean macrosyllable durations are 3.7 and 7.5 ms for the three and six syllable macrosyllables respectively. The song segment shown from the Strzelecki Desert (Fig. 7D) also exhibits a transition from three to six syllables within the macrosyllables, the mean macrosyllable durations being 3.4 and 7.0 ms, respectively.

The songs from these four locations are very similar, the main variable being the number of syllables per macrosyllable, either three or six. Even these, however, do interchange within the same song. As shown in Table 2, the
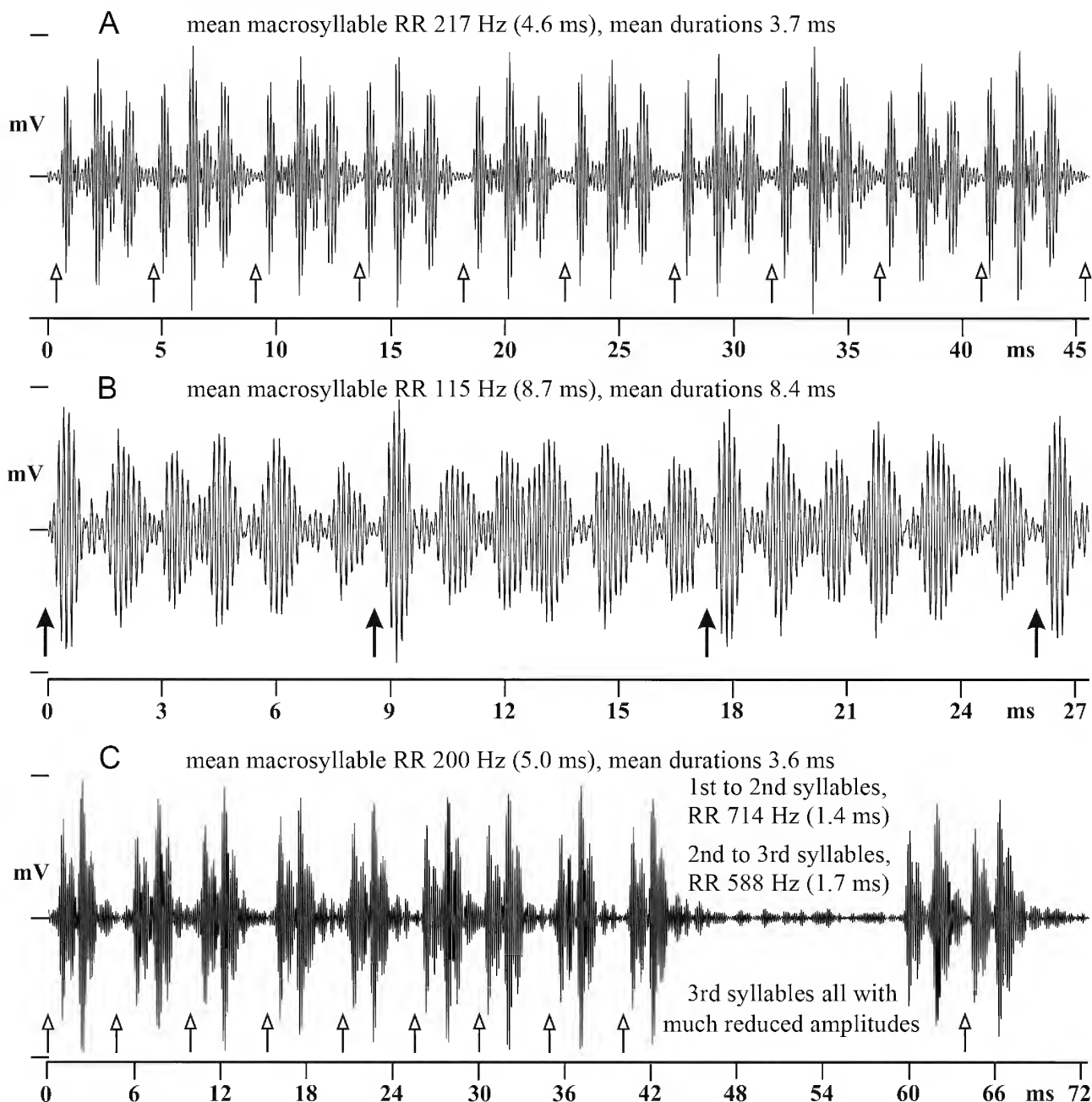
Figure 6. *Arenopsaltria nubivena*, waveform plots of calling songs from 19 km east-southeast of Windorah, southwest Queensland. *(A)* song segment with three dominant syllables in each macrosyllable, the hollow arrows marking the macrosyllable limits; *(B)* time expanded segment of three macrosyllables each with six dominant syllables, the limits of each marked by the arrows; *(C)* end segment of an extended buzzing element showing macrosyllables (limits marked by arrows) with three syllables, but with the third syllable having a strong reduction in amplitude; following the buzz element, separated by 17 ms, is a macrosyllable comprising three syllables, the third syllable also strongly reduced in amplitude. Field recordings, filtered to 4 kHz.

measurements of the main temporal characters of the songs from the four regional locations exhibit overlap between these characters, consistent with the songs representing the same species. This receives further support from the estimated dominant frequencies of these songs, as seen in the respective amplitude spectra (Fig. 9C–F, also summarized in Table 2). The inferred dominant frequencies range from 7.4 to 8.2 kHz, and the frequency envelopes shown in Fig. 9 by the bars (marking the envelope in which the frequency range shows highest concentration of acoustic energy

emitted, which we interpret as giving an estimation of the song bandwidth). The bandwidths range from 2.3 to 4.1 kHz, also similar, the lowest values from the Eneabba song. The numerical values of these bandwidths are consistent with the relatively sedentary singing habits of this species, based on observations of numerous other Australian species (unpublished data) with similar behaviour.

One consistent feature shown by the amplitude spectra is the occurrence of a weak extension of the frequency spectra to higher frequencies of up to at least 15 kHz, well
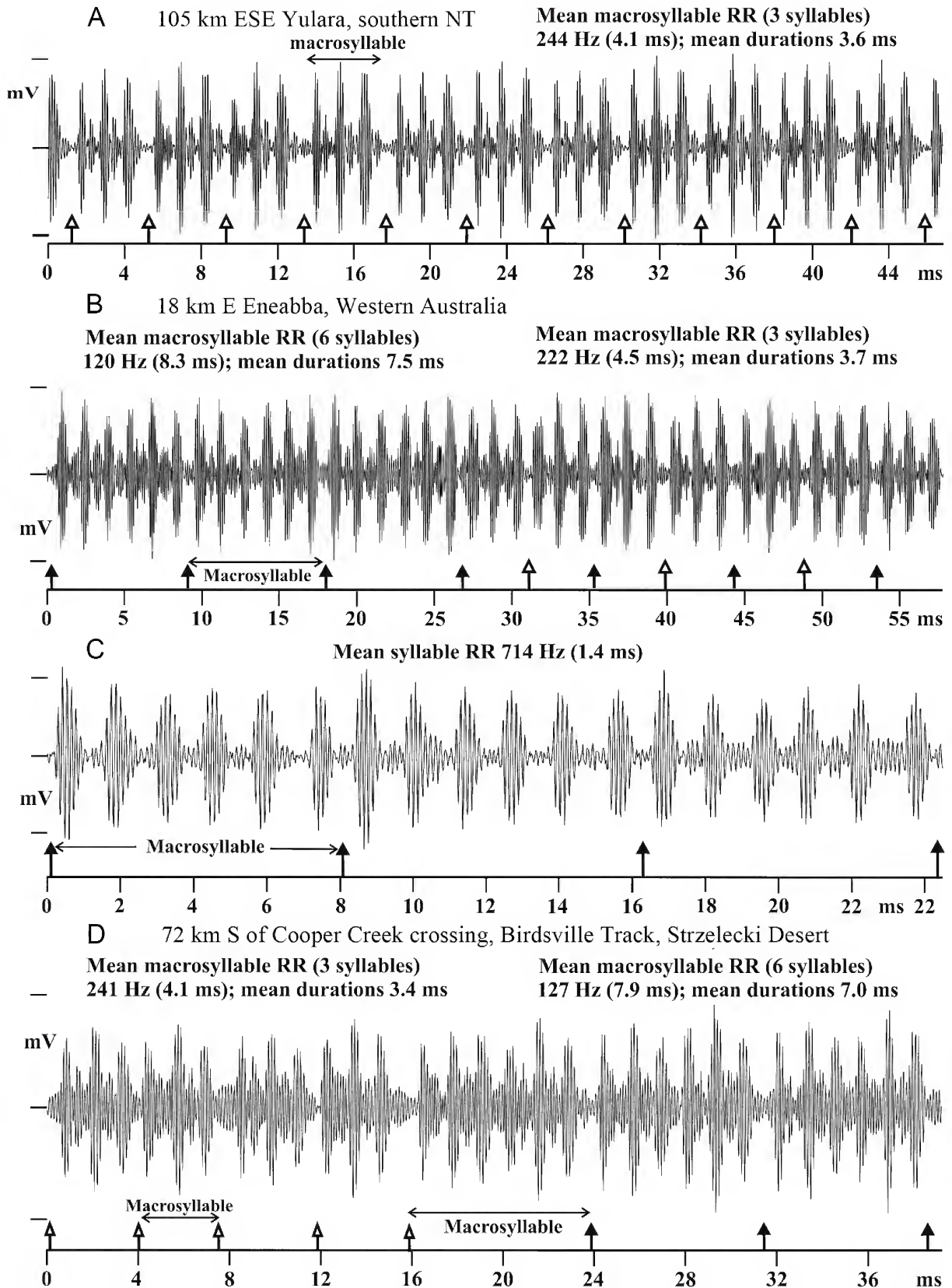
Figure 7. *Arenopsaltria nubivena*, waveform plots of calling songs from; *(A)* 105 km east-southeast of Yulara, southern Northern Territory, a higher resolution plot of buzzing element showing the macrosyllables, each with three dominant syllables, the hollow arrows marking the macrosyllable limits. *(B, C)* from 18 km east of Eneabba, southwestern Western Australia, higher resolution plots; *B*, showing a transition from initially six syllables per macrosyllable to three syllables per macrosyllable; *C*, further time expanded plot of three macrosyllables, each with six dominant syllables, the initiation of each macrosyllable marked by a higher amplitude syllable; *(D)* from 72 km south of Cooper Creek crossing, Birdsville Track, Strzelecki Desert, northeastern South Australia, showing macrosyllables with three and six dominant syllables, the arrows marking the macrosyllable limits. Field recordings, *A* filtered to 4 kHz, *B* to 5 kHz, *C* to 2 kHz, *D* to 1 kHz.
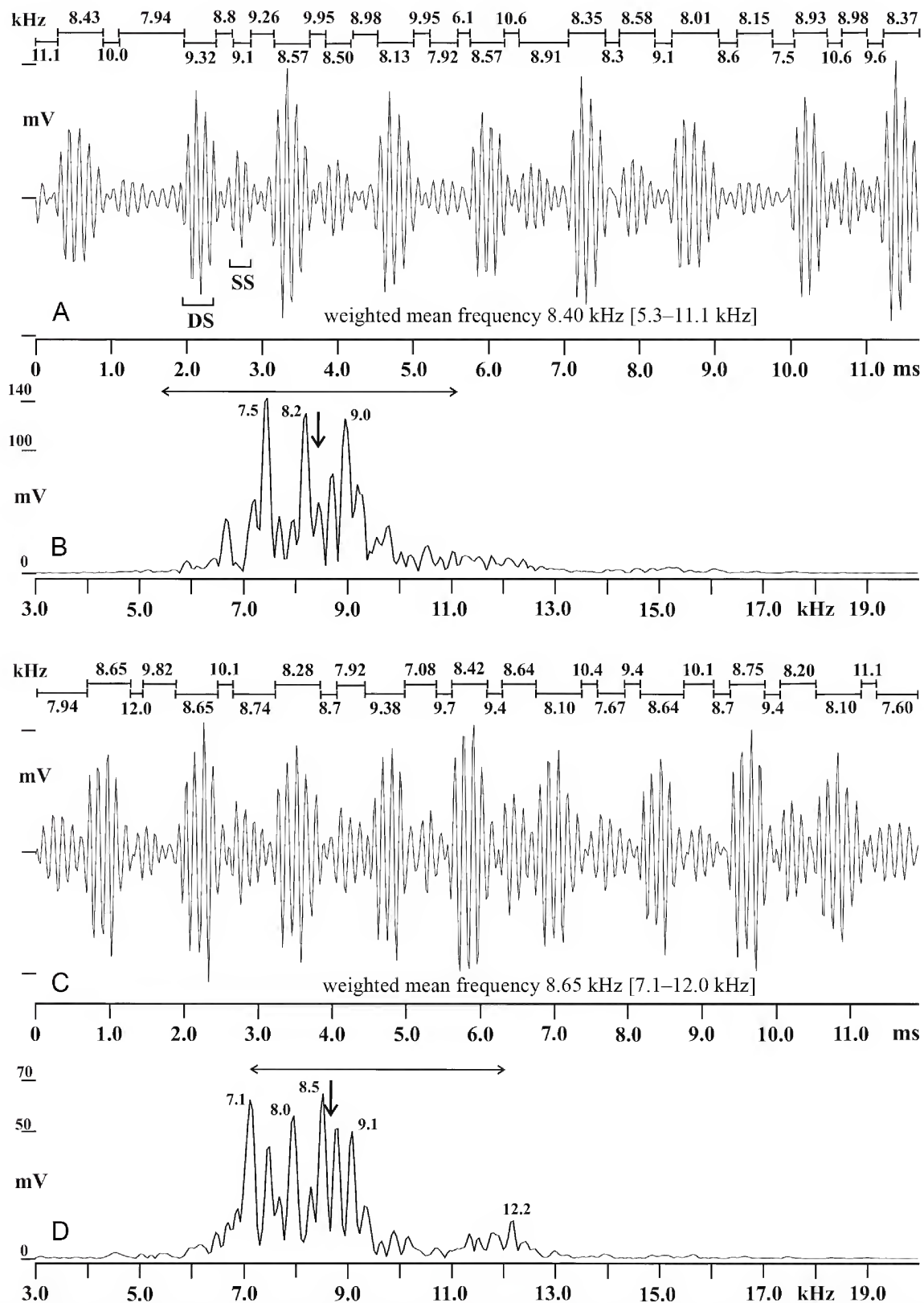
Figure 8. *Arenopsaltria nubivena*, higher resolution waveform and accompanying amplitude spectra plots of complete macrosyllables and segments of adjacent macrosyllables. The two recordings are of the calling songs, from 5.6 km west of Windorah, southwest Queensland. The macrosyllables each have six dominant syllables. *A* and *C* are waveform plots showing the high amplitude dominant syllables (labelled DS in *A*), these separated by smaller secondary syllables (labelled SS in *A*). Between these syllables are mostly low amplitude background pulses, possibly reverberation induced. The results of measurements on the carrier wave pulses are shown above the waveforms, showing the limits and calculated frequency (in kHz) within each of the short song segments, these mostly corresponding to the syllables and background pulses. *B* and *D* are the respective amplitude spectra of each of the two waveforms shown in *A* and *C*. The numbers adjacent to the selected spectral peaks are kHz. The measured frequency ranges (horizontal lines) and weighted mean frequency (downward pointing arrows), which are derived from the waveform plots, are shown. Song recordings filtered to 1 kHz.
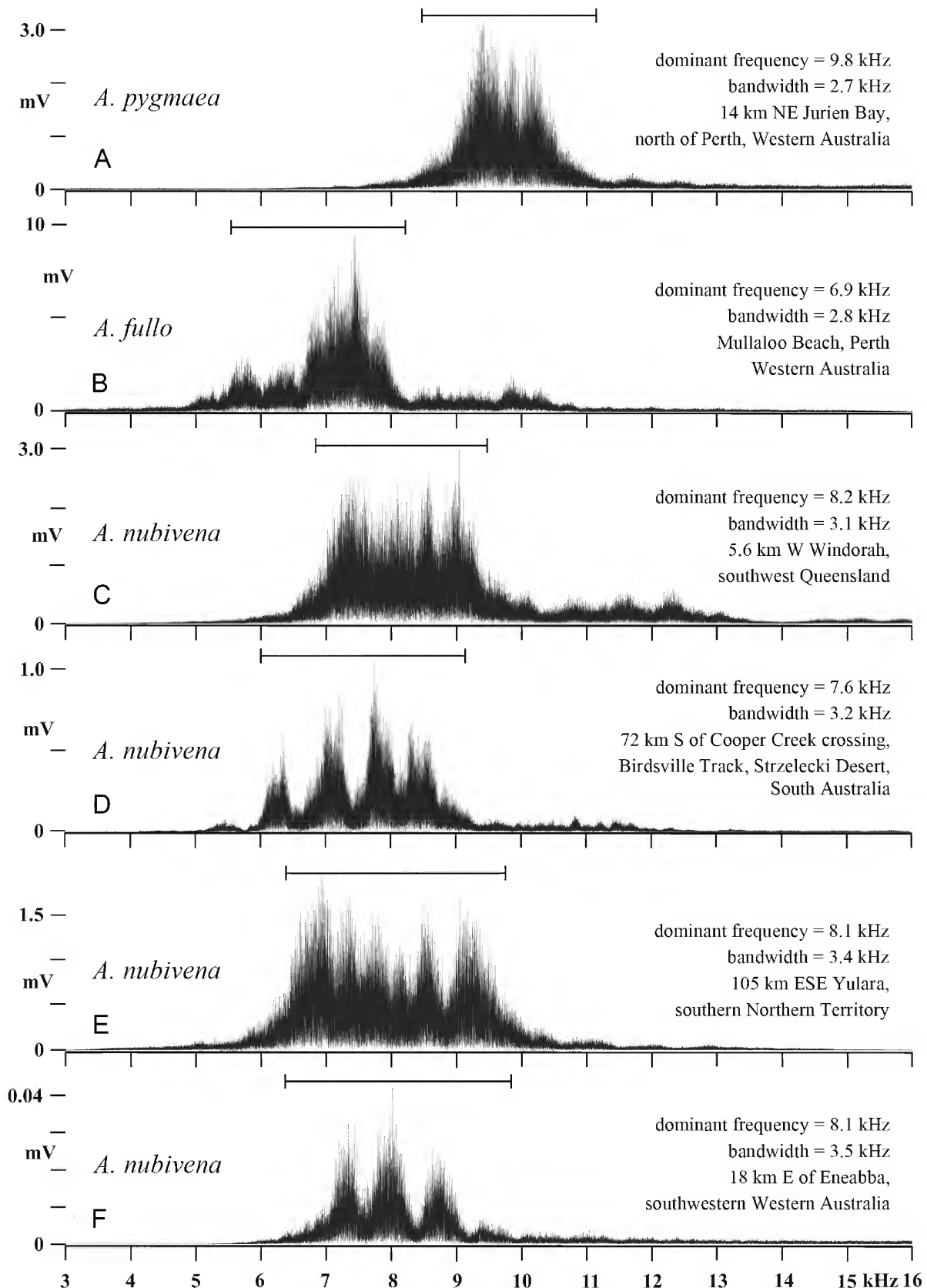
Figure 9. Comparative plots of amplitude spectra of: *(A) Arenopsaltria pygmaea* from 14 km northeast of Jurien Bay, Western Australia; *(B) Arenopsaltria fullo*, from Mullaloo Beach, north of Perth, Western Australia; *(C–F) Arenopsaltria nubivena*, from, respectively; 5.6 km west of Windorah, southwest Queensland; 72 km south of Cooper Creek crossing, Birdsville Track, Strzelecki Desert, South Australia; 105 km east southeast of Yulara, southern Northern Territory; and 18 km east of Eneabba, Western Australia, respectively. Note the weak extensions in all the plots to frequencies higher than the defined dominant frequency. The horizontal bars define the high amplitude frequency envelope of each spectrum, used to estimate the dominant frequency and the nominal bandwidth of each song. Each spectrum shown only between 3 to 16 kHz.

above the dominant frequency envelopes. These cannot be attributed to interference by background songs of other insects. These higher frequencies are also visible in high resolution waveform plots (Fig. 8) of selected segments from two calling song from 5.6 km west of Windorah, nine dominant syllables shown in both plots. The repetition rates of these carrier wave pulses have been measured on these plots, the results tabulated above the relevant segments in Fig. 8, showing the constantly changing "micro frequencies" as song emission progresses, the changes sometimes occurring on scales as short as 0.2 ms. Visual examination of these waveform plots suggests that the different syllable and inter-syllable components within the song do exhibit differing ranges of frequencies of the carrier pulses. To evaluate this further, measurements have been made on segments from five separate song recordings from this same location. The three components measured (Fig. 8A) are, first, the frequencies of the carrier pulses defining the dominant high amplitude syllables, secondly those defining the lower amplitude secondary syllables between the dominant syllables, and thirdly within the mostly low amplitude background pulses between the dominant and secondary syllables. The following results, expressed in kHz, are the means, 1s, and ranges. The values are, respectively: 8.46, 0.35, 7.78–9.38, n = 39; 8.32, 0.57, 7.08–9.36, n = 38; and 9.51, 1.99, 5.29–17.5, n = 63. These indicate that the pulses within the dominant and secondary syllables have similar frequencies and similar frequency ranges, and we suggest that the secondary syllables may represent the relaxation of the timbals and ribs following the emission of the dominant syllables. In contrast, the background pulses exhibit greater frequency ranges, extending to lower and especially to higher frequencies, feasibly produced by reverberation. The data in Fig. 8 indicate that the highest frequencies often occur immediately following the syllables. Whether they also occur within the syllables cannot be unambiguously assessed. The frequency ranges and magnitudes are consistent with their relevant amplitude spectra shown alongside the waveform plots in Fig. 8B and 8D, suggesting that the methodology is appropriate. The results confirm that the higher frequency, low amplitude tails observed in the amplitude spectra do represent an integral wave component within the carrier waves of the calling songs.

Calling songs of
Arenopsaltria fullo and *A. pygmaea*

Figs 10, 11; Table 3

For comparative purposes, the calling songs from the other two described *Arenopsaltria* species are here described, both species known only from coastal and near coastal areas of Western Australia (Moulds, 1990). The calling song of *A. fullo*, the type species of *Arenopsaltria*, was recorded at Mullaloo Beach, near Perth, Western Australia (see also Gwynne *et al.*, 1988). The extended buzz (Fig. 10A), when seen in time expanded waveforms (Fig. 10B), clearly shows well defined repeated macrosyllables, each longer and more clearly separated than in the song of *A. nubivena*.

The macrosyllables normally comprise 10 syllables, these occurring as well defined syllable doublets (Fig. 10B, C). In some macrosyllables, however, an additional single syllable occurs at the end of each macrosyllable. Comparison with the calling song of *A. nubivena* (Table 3) shows the *A. fullo* song to be dominated by macrosyllables with lower repetition rates (c.35 Hz), longer durations, higher numbers of syllables per macrosyllable, and slightly lower syllable repetition rates. The respective amplitude spectra (Figs 9B and 9C) indicate a lower dominant frequency (6.9 kHz) for the *A. fullo* song, although with similar bandwidths. The *A. fullo* spectrum also shows the weaker extension to higher frequencies to near 11 kHz, as seen in the *A. nubivena* songs.

Arenopsaltria pygmaea emits an extended buzzing song (Fig. 11, Table 3) with temporal structure similar to that of *A. fullo*, containing repeated macrosyllables, each with 11 to 18 discrete syllables. Compared to *A. fullo*, the macrosyllable repetition rates and durations are similar, while the syllable repetition rate and the number of syllables in the macrosyllables are higher. The song dominant frequency is also higher than in *A. fullo*, this correlating with the smaller size of *A. pygmaea* (Moulds, 1990).

Discussion of the calling songs. Although the songs of the three *Arenopsaltria* are aurally continuous buzzing songs, the detailed syllable and macrosyllable structures clearly distinguish the *A. nubivena* songs from those of *A. fullo* and *A. pygmaea*. This is in accord with the markedly different overall distribution patterns of the three species: *A. fullo* and *A. pygmaea* are relatively localized to coastal and subcoastal Western Australia, while *A. nubivena* has a broad distribution across much of arid Australia, including inland deserts. Although the population of *A. nubivena* in the southwestern area of Western Australia is outside the arid desert locations in which the other populations are found in the southern Northern Territory, northeastern South Australia, and southwestern Queensland, the southwestern Western Australian environment is characterized by open shrublands developed on relatively infertile sandy soils with remnant dunes. Whether the *A. nubivena* distribution actually extends continuously across the Western Australian deserts is unknown, and the populations in southwestern Western Australia may well be isolated in the southwestern corner. This is suggested by their apparent absence from the more arid, inland regions (Yilgarn region) of Western Australia. The observation presented here for the similarity of the songs of *A. nubivena* across much of their very extensive distribution indicates very little evolution of the songs, this perhaps indicative of relatively recent expansions of the cicada populations in response to expansions of the habitats that contain them.

It is nevertheless noted that, behaviourally, the three *Arenopsaltria* species are relatively localized species, remaining mainly sedentary when calling with no strong tendency towards "sing and fly" behaviour. They do, however, emerge in large numbers with appropriate timing and density of rainfall. Nothing is known, however, concerning the dispersal behaviour of the *A. nubivena* females. Field observations indicate that monotonous, continuous buzzing songs are characteristic of sedentary singing behaviour in Australian cicadas.
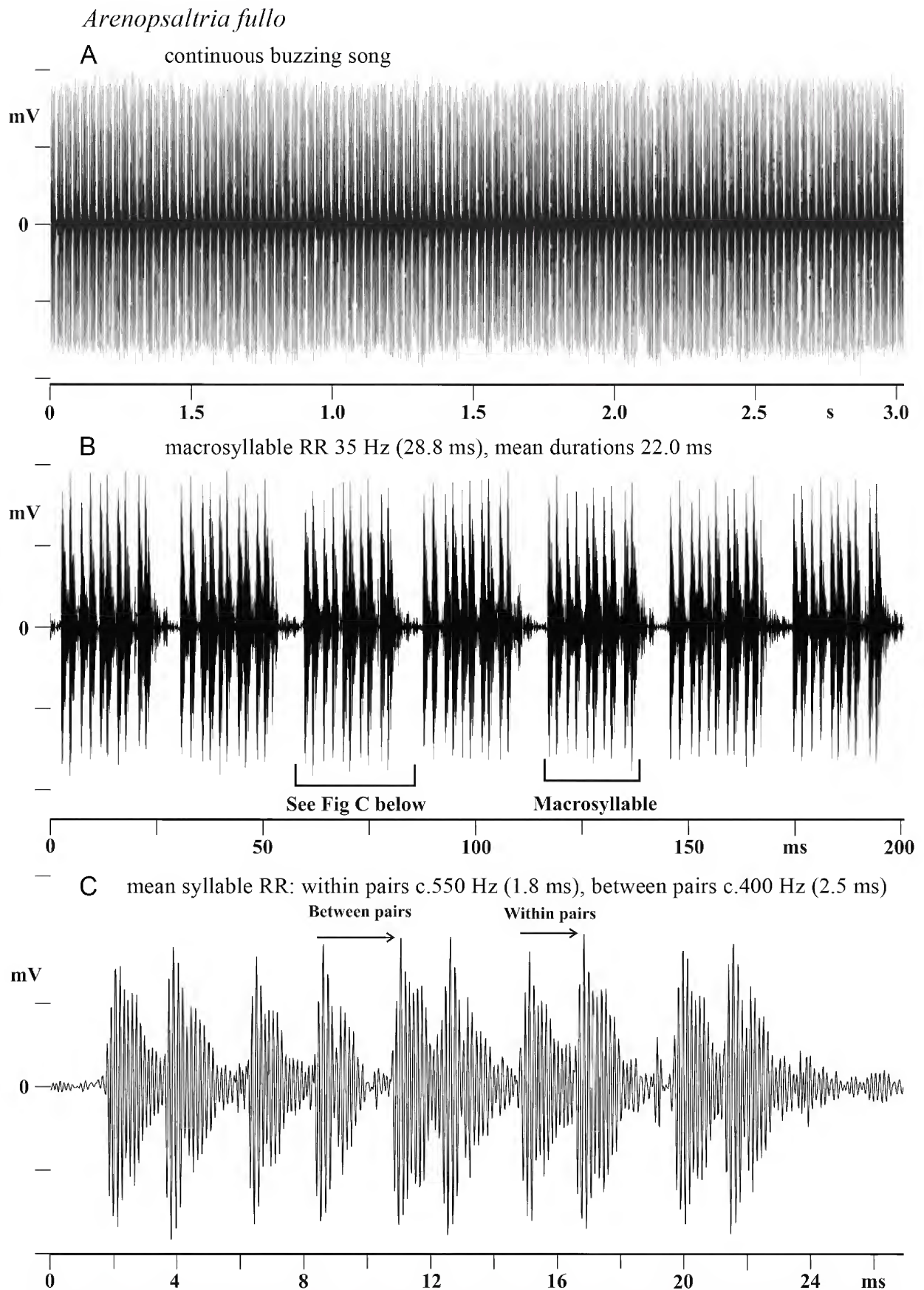
Arenopsaltria fullo

A   continuous buzzing song

B   macrosyllable RR 35 Hz (28.8 ms), mean durations 22.0 ms

See Fig C below   **Macrosyllable**

C   mean syllable RR: within pairs c.550 Hz (1.8 ms), between pairs c.400 Hz (2.5 ms)

Between pairs   Within pairs

Figure 10. *Arenopsaltria fullo*, waveform plot of calling song from Mullaloo Beach, Perth, Western Australia. *(A)* general view of continuous buzzing song clearly exhibiting division into discrete macrosyllables; *(B)* time expanded view showing more detail of the macrosyllable structures, each comprised of five pairs of double syllables; *(C)* higher resolution view of a single macrosyllable showing more detail of the five double syllables. Field recording, unfiltered.
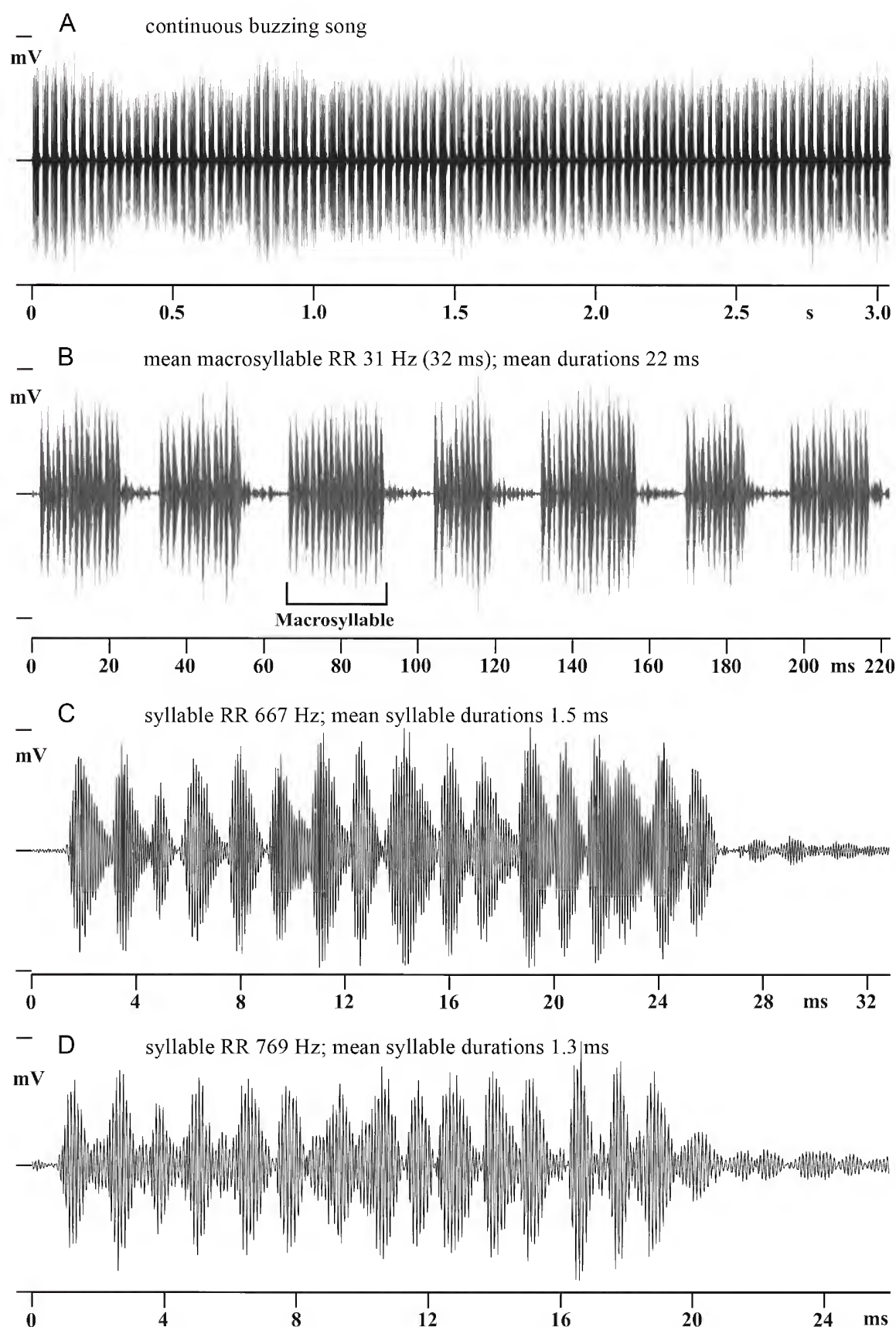
Figure 11. *Arenopsaltria pygmaea*, waveform plot of calling song from 14 km northeast of Jurien Bay, Western Australia. *(A)* general view of continuous buzzing song clearly exhibiting the discrete macrosyllables; *(B)* time expanded view showing more detail of the macrosyllable structures, each comprised of between 11 to 18 syllables; *(C, D)* higher resolution plots of a single macrosyllable from two separate recordings showing more detail of the syllables. Field recordings, filtered to 3 kHz.
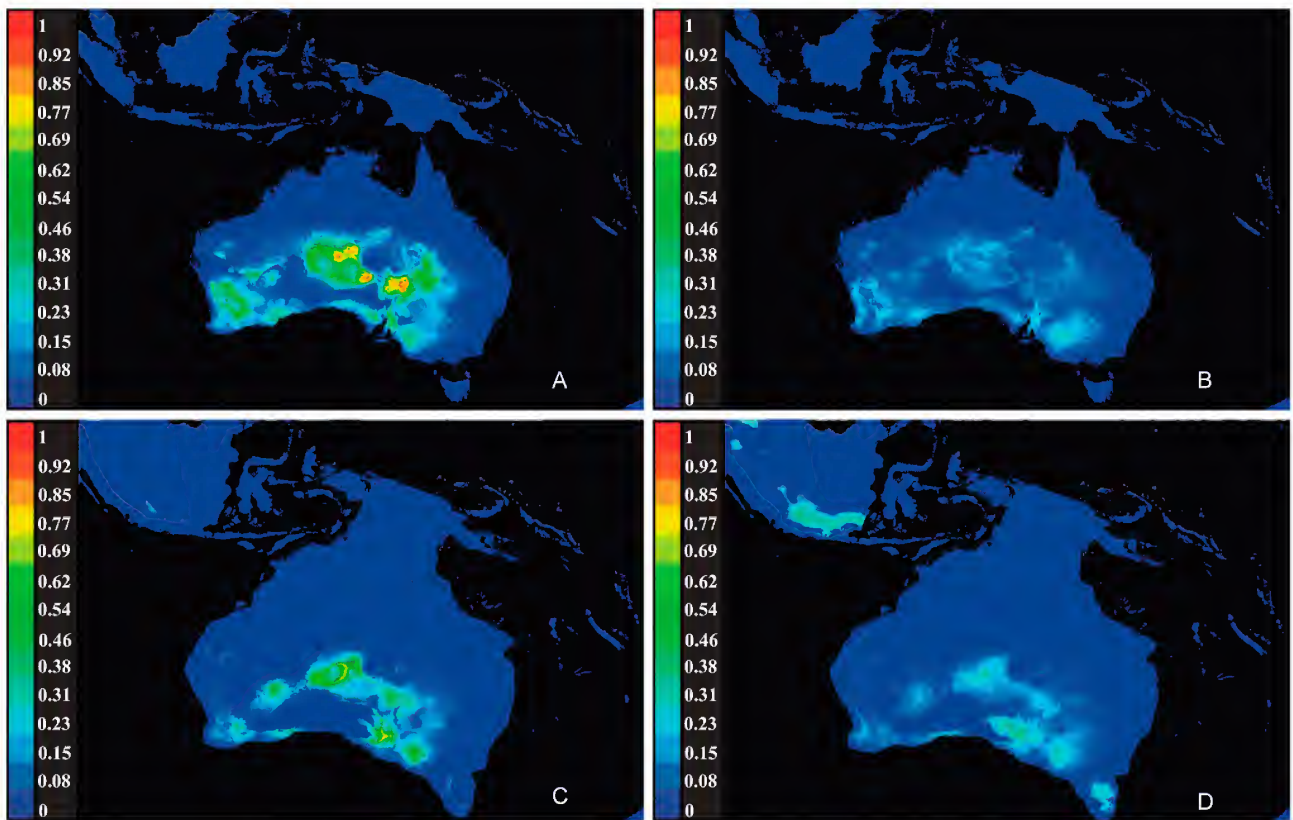
Figure 12. Species Climatic Envelope (SCE) models for *Arenopsaltria nubivena* produced using MaxEnt: *(A)* present day (1950–2000) model; *(B)* standard deviation of the present day model; *(C)* Last Glacial Maximum (LGM) projection; *(D)* standard deviation of the LGM projection. The coloured columns labelled 1 to 10 represent the raw outputs from an exponential function of the probability of occurrence (with 1 equal to 100% modelled likelihood of occurrence). The standard deviation maps depict variation in the model between 10 independent runs. Areas with a higher standard deviation varied more strongly in predicted climatic suitability for the species between different runs.

MaxEnt modelling of *Arenopsaltria nubivena* distribution

Fig. 12

Methodology. Specimen records, aided with calling song recordings, confirm that *Arenopsaltria nubivena* is a widespread species across arid and semi-arid areas within Australia, as documented above. The available geographical data provide a basis for exploratory climatic modelling. Such modelling has the potential to reveal distributional changes since the Last Glacial maximum (LGM), and is useful for revealing areas where the species may currently occur in the absence of record data and even potential refugia. We focus on the period of the climatic extremes between the LGM (c. 22 ka) to the present, a period of time when the climate changed from extreme cooling and aridity towards the relative warmth and higher humidity of the Holocene. We regard this period as most likely having the most severe and influential effects on the distributions of species, in this case, specifically relevant to *A. nubivena*.

To evaluate the above patterns, the current and past distributions of *A. nubivena* were estimated by generating ecological niche models using MaxEnt 3.3.3k (Phillips *et al.*, 2006; Phillips & Dudik, 2008). In this case, available data were restricted to variables pertaining to climate only and as such the particular model developed here need

technically be treated as a species climatic envelope (SCE), rather than a complete model of the ecological niche. Climate data used to construct the SCEs were sourced from *WorldClim* (Hijmans *et al.*, 2005) and included the original 19 BIOCLIM climate attributes for the present day (1950–2000) and complementary past climate data for the last glacial maximum (LGM) at c. 22 ka before present. To reduce the risk of multicollinearity having a strong influence on the outcome and interpretation of the analyses (Dormann *et al.*, 2013), Pearson's correlation coefficient analyses were performed on these climate data. A conservative value of $\geq$ ±0.85 was used to identify highly correlated variables (Elith *et al.*, 2010). The following 10 BIOCLIM climate attributes were retained:

BIO1 = Annual Mean Temperature
BIO2 = Mean Diurnal Range (Mean of monthly max–min temp)
BIO5 = Max. Temperature of Warmest Month
BIO6 = Min. Temperature of Coldest Month
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of Driest Quarter
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO15 = Precipitation Seasonality (Coefficient of Variation)
BIO18 = Precipitation of Warmest Quarter

Climatic envelope models were built using 26 unique distribution records for the species. The approach to the

analysis follows that of Marshall *et al.* (2012). Maximum iterations were increased to 1000 to allow the algorithm to converge, with default settings applied otherwise. The model was performed in 10 independent runs. To ensure repeatability and consistency of model predictions across multiple runs, 10% of records were randomly assigned as test points for each run, so that each record was used to test the model once. In each run, estimated models were then projected on to LGM climate surfaces. The "fade by clamping" setting was specified for output grids, which allowed inconsistencies in spatial predictions between different runs to be more accurately revealed in the combined analysis. Final geographical projections were based on the mean point-wise prediction over the 10 model runs. Model performance was assessed using threshold dependent binomial omission tests and the Area Under the (Receiver Operating Characteristic) Curve (AUC) calculated by MaxEnt.

Results and discussion. The MaxEnt model for the SCE of *A. nubivena* performed significantly better than random in all 10 runs and returned an AUC average of 0.969 (±0.008), indicative of a robust model. Three climate variables were identified as contributing most strongly to the model (>14% influence to final output). These were BIO13 = Precipitation of Wettest Month (29.8%); BIO18 = Precipitation of Warmest Quarter (18.6%); and BIO14 = Precipitation of Driest Month (14.9%). Of these, the spatial representation of BIO13 was identified by Jacknife analysis (a component of the MaxEnt output) as corresponding most strongly with the model distribution when used in isolation, which therefore appears to have the most useful information by itself. The environmental variable that reduces the most gain when it is omitted is BIO14, and which therefore appears to have the most information that is not present in the other variables. Values shown are averages over replicate runs. The three variables that have the greatest contribution to the model are precipitation variables.

As documented above, *A. nubivena* has a strong association with dunes and dunefields, indicative of an arid to semi-arid adapted species. Climatically, the LGM was cooler and more arid than the present climate. Notwithstanding, the climate modelling predicts a present day northerly expansion of the distribution of *A. nubivena* relative to the LGM, most strongly pronounced into southwest Queensland, an area where the modelling suggests its absence at the LGM. An expansion is also predicted on the sandplains of southwestern Western Australia, while a potentially suitable climate surface is predicted covering a slightly enlarged region in western New South Wales, as compared to the LGM, noting, however, that no specimens are currently reported from the latter region. We suggest that the present day modelled distribution patterns are broadly consistent with the modelled dependence on more extensive rainfall, also coupled with warming temperatures (variable BIO18), noting that *A. nubivena* currently occurs in the warm to temperate margins of the arid zone, areas which experience sporadic, although often heavy, seasonal summer rainfall events. Collections and observations indicate that extensive emergences of *A. nubivena* occur after such rain events. It is relevant to compare the modelled distribution of *A. nubivena* with that of another, more strongly arid adapted

species, *Simona erema* (Ewart *et al.*, 2015). For *S. erema*, comparable modelling actually predicts a decrease in distribution range of the latter species at the present time compared to the LGM.

The above modelled and observed distribution patterns of *A. nubivena* need also be reconciled with the observed present day geographical distribution of dunefields in Australia, the distributions of which have been related most closely to topography, climate and substrate (Hesse, 2010). The more easterly dune systems (Simpson, Strzelecki and Mallee Deserts) lie on extensive, relatively flat Neogene sedimentary basins which provide plentiful sand supplies and significantly contain multiple known occurrences of *A. nubivena*. In contrast, the more western deserts (Great Victoria and Sandy) lie on hardened, less easily eroded older Proterozoic to Mesozoic sediments with reduced sand supply. *Arenopsaltria nibivena* is not currently recorded from these desert areas. Further southwest is the Yilgarn region of southwest Western Australia which is located on even older, deeply weathered Archaean granitic and ultramafic basements, which provide poor sand supplies and which have resulted in the formation of widespread smaller dune systems (Hesse, 2010). Localized occurrences of *A. nubivena* occur on dune remnants in the southwestern segment of this region. The Nullarbor Plain, in contrast, may provide an extreme example, largely devoid of dunes, and, based on collections and modelling, evidently devoid of *A. nubivena* (Figs 2 and 12). Late Quaternary dune formation was more active during the Late Pleistocene than at the present time, resulting in the development of dunes in some relatively humid areas around continental fringes, areas which are now climatically unsuitable for dune formation (Hesse, 2010). The southwestern corner of Western Australia provides one such example.

A further critical factor is vegetation. Modern Australian dunefields are generally relatively well vegetated, and in the modern climatic regime relatively stable. Dunkerley (2010) has drawn attention to the importance of plants in mediating the impacts of Quaternary and Holocene climate change, and this factor may, by default, be hidden in the known distribution data input mode to the modelling process. It is anticipated that vegetation cover will have increased in both extent and density between the LGM and the present time, in response to increased warming and precipitation. Available luminescence dates of Australian dune systems, which most likely represent stabilization ages (summarized in Fujioka & Chappell, 2010), confirm that extensive stabilization has occurred during the past 20 ka.

In summary the modelling predicts the existence of a suitable climate surface for this species over relatively extensive regions of southern Australia, both at the time of the LGM and the present day. The model predictions are broadly consistent with the documented climatic changes that have occurred between those intervals (e.g., Hess *et al.*, 2004), the geomorphological and stabilization histories of dunefields through central and southwestern Australia, and the accompanying increasing vegetation cover. The progressive change towards the modern climate was marked by climatic oscillations, possibly suitable for the preservation of scattered refugia (e.g., Byrne, 2008). Details of the geographic distributions will, nevertheless, also be mediated by additional factors such as dispersal barriers and inter-specific interactions.

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